# Small-scale biogeographical patterns in some groundwater Crustacea, the syncarid, Parabathynellidae.

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**Abstract.** An analysis was made of the micro-distribution patterns of five phylogenetically closely related species belonging to the genus *Iberobathynella*, a group of subterranean aquatic crustaceans (Syncarida, Parabathynellidae). The two-step model of colonization and speciation seems to provide a valid explanation for the current distribution of a large number of stygobiontic taxa of marine origin (thalassoid). However, with respect to the *Iberobathynella*, only the colonization of the subterranean environment at the mesoscale level can be explained. The second phase of the model, marine regression, can only explain the colonization of the region by the ancestor; the subsequent evolution and speciation at a smaller scale remain to be explained. Local geological constraints – Upper Triassic gypsiferous mudstone deposits plus faults and thrusting linked to the Alpine Orogeny – are responsible for the appearance of local palaeogeographic phenomena. These may have been the vicariant processes responsible for the geographical and genetic isolation of the ancestral populations of this group, which eventually led to clade divergence. Together with small-scale passive dispersion (11 dispersal events) and local extinction, these processes could be responsible for the current distribution of the five sister taxa inhabiting the caves of the Sierra de la Collada, Spain. A plausible palaeogeographical scenario is offered to explain their present distribution, that clearly came about through chance events.

## Introduction

The study of the distribution of organisms is easily extended from the 'macro-picture' (the distribution of higher taxonomic units over large areas) to the 'micro-picture' (the distribution of species and subspecific taxa over smaller regions and local areas). Both distributions may respond to the same pattern-inducing forces, although more local determinants may be involved in the formation of the micro-picture.

Until recently, it was a paradigm of environmental biology (ecology, biogeography and the like) that if the processes affecting organisms were to be studied, large numbers of these organisms should be available for observation. This was certainly a requirement of the statistical techniques (mainly

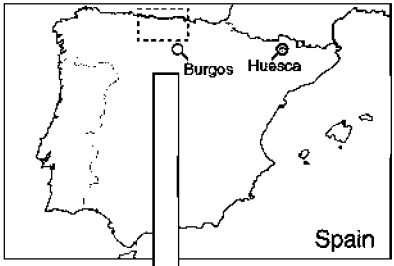
parametric statistics) used in such studies. Nowadays, however, new methodologies and powerful computers are providing alternative approaches. Many taxa are very rare – or at least appear to be when usual sampling methods are used. Indeed, there are more 'rare' than 'common' taxa, yet many quantitative environmental methodologies were developed for use with these more abundant forms. There is no reason, however, why less abundant groups cannot be used to help answer fundamental biological questions, although It may be harder to make them 'speak out'.

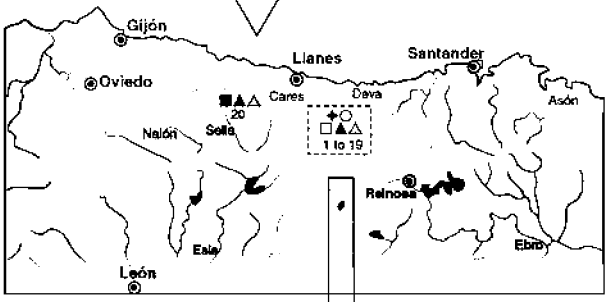
The family Parabathynellidae is a group of crustaceans (Arthropoda, Syncarida) that live almost exclusively in subterranean water (in caves and the interstitial environments). Representatives of the family are found all over the world, except for the North and South Polar regions. Within this family, the Iberobathynellini (Camacho and Serban 1998). Tribe comprise 26 species grouped into six genera that inhabit the Iberian Peninsula, the Balearic Islands, the south of France, North Africa (the Maghreb) and North America. The genus *Iberobathynella* (Schminke 1973; Camacho and Serban 1998), only inhabits the Iberian Peninsula (Camacho and Serban 2000; Camacho 2003a, b). This comprises three subgenera and 18 species (four recently described); its distribution and abundance has been previously discussed (Camacho 2003b). Five species are limited to a small area in the northern Iberian Peninsula: *Iberobathynella* (*Espanobathynella*) *cantabriensis* Camacho and Serban (1998), *I.* (*E.*) *magna* Camacho and Serban (1998) *Iberobathynella* (*Asturibathynella*) *asturiensis* Serban and Comasi Navarro (1978), *I.* (*A.*) *parasturiensis* Camacho and Serban (1998), and *I.* (*A.*) *imuniensis* Camacho (1987) [this species can be found as far South as Burgos and as far East as Huesca (Figure 1)]. It is remarkable that, being a very rare group, five species of two subgenera should be found in such a small area. Phylogenetically these species are very closely related, and their distribution is reduced (characterized by low local densities and a limited dispersion capacity). It is therefore to be expected that the degree of speciation is high (Gavrilets and Vose 2000).

Previous analyses on syncarid distribution have focused on the world-wide or continental scales (Schminke 1974; Camacho et al. 2000; Guil and Camacho 2001) and models have been proposed to explain their macro-picture pattern. It is tempting to determine whether similar processes might satisfactorily explain their micro-picture. The purpose of this work is to determine whether their distribution pattern is significantly different from random, and, if so, to determine the relationship between the areas where they are found and the phylogeny of the species.

## Material and methods

The study area was the Sierra de la Collada located near the Picos de Europa between Cantabria and Asturias in Spain's Cantabrian Range. It is an area with natural geographical limits, bound by the River Deva to the West and the




General area

Specific area

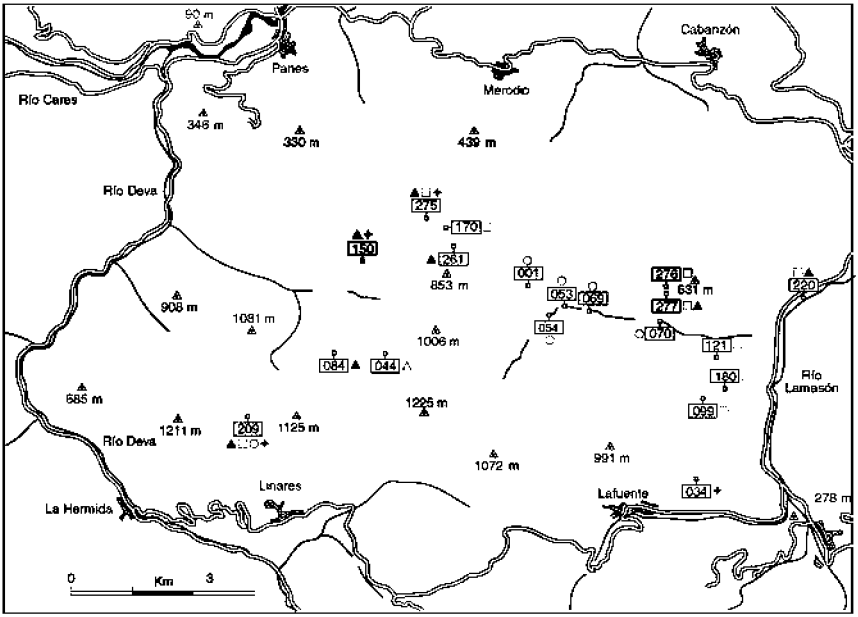


*Table 1.* Localities and species distribution in the Sierra de la Collada (Asturias/Cantabria)

| Name | Locality | Province | Area | UTM | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|---|---|---|---|
| CO.001 Hoyu | Panes | Asturias | d | 30TUN7594 | 0 | 0 | 1 | 0 | 0 |
| CO.034 Nava | Lamasón | Cantabria | e | 30TUN7890 | 0 | 1 | 0 | 0 | 0 |
| CO.044 Tresavarilla | Peñarrubia | Cantabria | b | 30TUN7392 | 1 | 0 | 0 | 0 | 0 |
| CO.053 Huerta | Panes | Asturias | d | 30TUN7693 | 0 | 0 | 1 | 0 | 0 |
| CO.054 Seguedal | Panes | Asturias | d | 30TUN7593 | 0 | 0 | 1 | 0 | 0 |
| CO.069 Pozo | Panes | Asturias | d | 30TUN7693 | 0 | 0 | 1 | 0 | 0 |
| CO.070 Cincho | Herrerias | Cantabria | d | 30TUN7793 | 0 | 0 | 1 | 0 | 0 |
| CO.084 Helechosa | Peñarrubia | Cantabria | b | 30TUN7292 | 0 | 0 | 0 | 1 | 0 |
| CO.099 Calderón | Lamasón | Cantabria | e | 30TUN7892 | 0 | 0 | 0 | 0 | 1* |
| CO.121 Torcas | Lamasón | Cantabria | e | 30TUN7892 | 0 | 0 | 0 | 0 | 1 |
| CO.150 Grañaja | Peñarrubia | Cantabria | c | 30TUN7294 | 0 | 1 | 0 | 1 | 0 |
| CO.170 Indiano | Panes | Asturias | c | 30TUN7495 | 0 | 0 | 0 | 0 | 1 |
| CO.180 Sotombos | Lamasón | Cantabria | e | 30TUN7892 | 0 | 0 | 0 | 0 | 1 |
| CO.209 Treslajorá | Peñarrubia | Cantabria | a | 30TUN7091 | 0 | 1* | 1 | 1 | 1 |
| CO.220 Carnero | Herrerías | Cantabria | e | 30TUN8093 | 0 | 0 | 0 | 1 | 1 |
| CO.261 Pelacristo | Panes | Asturias | c | 30TUN7494 | 0 | 0 | 0 | 1 | 0 |
| CO.275 Divisada | Panes | Asturias | c | 30TUN7395 | 0 | 1 | 0 | 1 | 1 |
| CO.276 Torco | Herrerías | Cantabria | e | 30TUN7794 | 0 | 0 | 0 | 0 | 1 |
| CO.277 Lobos | Herrerías | Cantabria | e | 30TUN7794 | 0 | 0 | 0 | 1 | 1 |
| | | | | | 1 | 4 | 6 | 7 | 9 |

Number and name of locality, locality, province, area, UTM. 0 = absence and 1 = presence of the species 1 = *I.* (*A.*) *asturiensis* (Serban and Comas 1978), 2 = *I.* (*A.*) *parasturiensis* (Camacho and Serban 1998), 3 = *I.* (*A.*) *imuniensis*(Camacho 1987), 4 = *I.* (*E.*) *magna*(Camacho and Serban 1998), 5 = *I.* (*E.*) *cantabriensis* (Camacho and Serban 1998). *Type locality for the species.

River Lamasón to the East (Figure 1). The Sierra de la Collada is an eastern extension of the massive rocky formations of the Carboniferous produced by the Alpine Orogeny (the Eastern Massif of the Picos de Europa). All caves in the area offering a suitable habitat for bathynels were sampled ($n$ = 35). Five species of the *Iberobathynella* Schminke (1973) genus were found, distributed in 19 caves (Table 1 lists these caves and indicates which species inhabit them).

Figure 1 provides an outline of the area, its location in the Iberian Peninsula and the location of the caves. Figure 2 is a more detailed map of the area, which includes the geological subdivisions, the locations of the 19 caves, and the species present in each.

Before studying the possible dependence of the distribution of these species on the geological nature and history of the area, we tested whether it was significantly different from random using the Anosim non-parametric test. This test is frequently employed in ecological research (Clarke and Green 1988). The

*Figure 1.* Map of study area (North of the Iberian Peninsula, Cantabrian Region and Sierra de la Collada) at both small and large scales, showing the distribution of species in detail: *Iberobathynella* Schminke (1973) species of the subgenera *Asturibathynella* Camacho and Serban (1998) and *Espanobathynella* Camacho and Serban (1998). Each number corresponds to a site in Table 1. Species codes as in Figure 2.

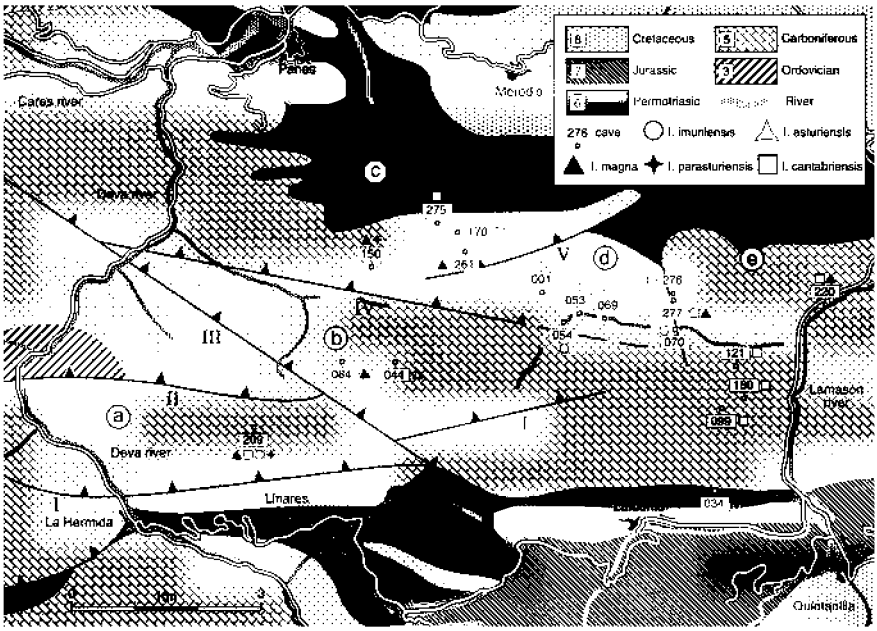



*Figure 2.* Limits of the Sierra de la Collada; geological and paleogeographical evolution; location of the caves and distribution of *Iberobathynella* Schminke (1973) species. Roman numbers denote the location of the faults. 'a' to 'e' areas delimited by faults.

null hypothesis assumes there are no differences between the areas, and this was tested by calculating an index '$R$' which contrasts between-area and within area rank similarities. ['Area' refers to the different sectors bounded by faults in the Sierra de la Collada; the different caves were assigned to each of these zones (labelled 'a' to 'e' in Table 1)].

$$\boldsymbol{R} = \frac{(\bar{r}_B - \bar{r}_W)}{\frac{1}{2}M}$$

where

$\bar{r}_B$ is the average rank of all similarities from all pairs of caves between areas,

$\bar{r}_W$ is the average of all rank similarities among caves within areas, and

$M = n(n-1)/2$ where $n$ is the total number of caves considered.

The closer the value of $R$ to 1, the more similar are the caves belonging to a particular area to caves of a different area. This index was recalculated using permutations and a significance level determined by comparing the observed value of $R$ to its permutation distribution. PRIMER version 5 software (Clarke and Warwick 2001) was used to determine cave similarity based on fauna analysis, to work out the multidimensional scaling ordination (MDS) based on rank order of similarities among caves, and to perform the Anosim test.

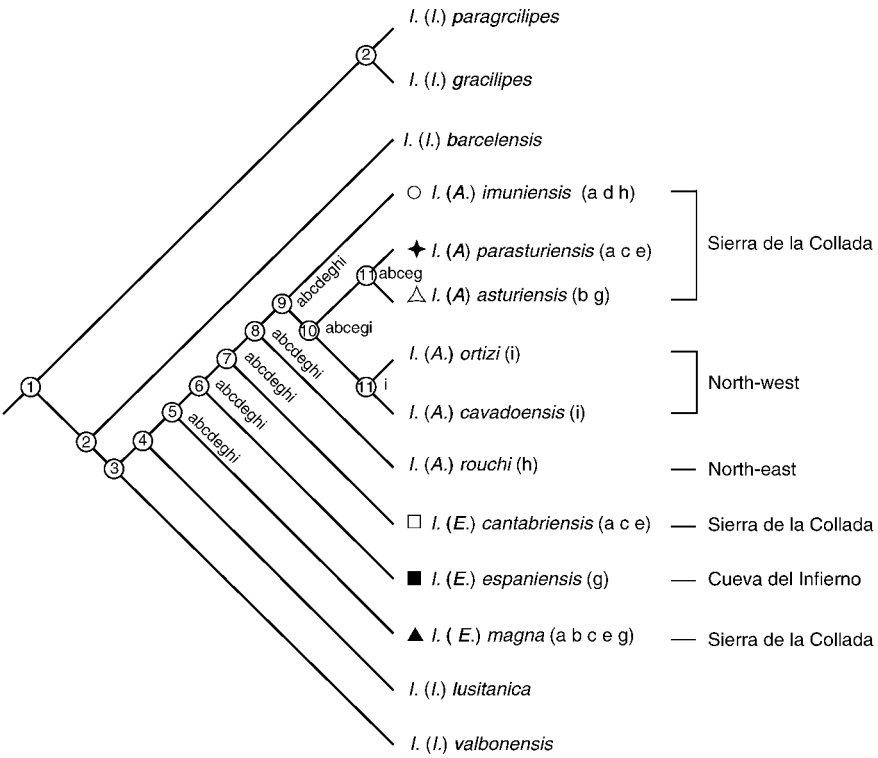



*Figure 3.* Cladogram of species of the *Iberobathynella* Schminke (1973) genus [after (Guil and Camacho 2001)], number of nodes and DIVA distribution on nodes. Small letters denote the areas quoted in Tables 1 and 2 ('a' to 'e' sectors in Sierra de la Collada and 'g' to 'i' areas outside Sierra de la Collada).

A morphological cladogram of 14 species of the genus *Iberobathynella* (Guil and Camacho 2001) (Figure 3) was used to portray the phylogenetic relationships between the five species discovered and their proximity to other species in this monophyletic group (Camacho and Serban 1998).

Dispersal-vicariance analysis (DIVA, Ronquist 1996, 1997a, b) minimizes the problems associated with the classic methodologies used in historical biogeography, especially the *ad hoc* construction of narrative scenarios of dispersal vicariances (Ronquist 1994, 1997a, b; Martín-Piera and Sanmartín 1999). The DIVA strategy adequately responded to the needs of this study, and was used to examine:

(1) the phylogenetic relationships among the five species from the study area plus four species from nearby areas;
(2) the distribution area of each of the five recorded species (Table 2, Figures 2 and 5).

DIVA is a quantitative method derived from trait optimisation methods (Fitch optimisation). It minimizes dispersion and extinction events and allows

*Table 2.* Area/species distribution in the Sierra de la Collada ('a' to 'e') and outlying areas (g, Cueva del Infierno, type locality of species 1, 4 and 6; h, North–East and i, North–West

| Area name | Delimitation between faults | Caves CO. | Species number |
|---|---|---|---|
| a | I/II/II | 209 | 2, 3, 4, 5 |
| b | I/III/IV | 44, 84 | 1, 4 |
| c | IV/V | 150, 170, 261, 275 | 2, 4, 5 |
| d | IV/V/VI | 1, 53, 54, 69, 70 | 3 |
| e | IV/VI | 220, 276, 277, 34, 99, 121, 180 | 2, 4, 5 |
| g | Outer | Cueva del Infierno | 1, 4, 6 |
| h | Outer | North-East | 3, 9 |
| i | Outer | North-West | 7, 8 |

1 = *I.* (*A.*) *asturiensis* (Serban and Comasi Navarro 1978), 2 = *I.* (*A.*) *parasturiensis* (Camacho and Serban 1998), 3 = *I.* (*A.*) *imuniensis* (Camacho 1987), 4 = *I.* (*E.*) *magna* (Camacho and Serban 1998), 5 = *I.* (*E.*) *cantabriensis* (Camacho and Serban 1998), 6 = *I.* (*E.*) *espaniensis* (Serban and Comasi Navarro 1978), 7 = *I.* (*A.*) *ortizi* (Camacho 1989), 8 = *I.* (*A.*) *cavadoensis* (Noodt and Galhano 1969), and 9 = *I.* (*A.*) *rouchi* (Camacho and Coineau 1987).

for multiple reticulated area relationships (not just single branching patterns). It requires no *a priori* assumptions about the existence of a unique biogeographical scenario, nor is it necessary to assume that ancestral species were generally more widespread than their descendants. The model assumes that distributions of current species and their ancestors can be described in terms of area groups.

As in other biogeographical reconstruction methods, the null hypothesis is based on allopatric speciation by geographic vicariance since, theoretically, allopatric speciation is the most common speciation mechanism (Mayr 1963; Futuyma and Mayer 1980; Ronquist 1997a, b). Empirical studies support this idea (Lynch 1989; Asquith 1993; Chesser and Zink 1994), although they also indicate that dispersion may play an important role. Both extinction and dispersion, which are unpredictable phenomena, can wipe out evidence of biogeographical vicariant processes and dispersal events that took place in contiguous areas. When the general vicariant events are known, connections and dispersal barriers between areas can be inferred from the different frequencies of the hypothetical ancestral distribution and dispersal events.

## Results

### *Palaeogeographic reconstruction*

The geological study of the area led to the following stratigraphic reconstruction (see Figure 4). The oldest deposits in the area (Lower Cambrian; 570 Myr) are composed of marine dolostones and algal limestones overlain by alternating layers of marine shales and sandstones, with emergent terres-

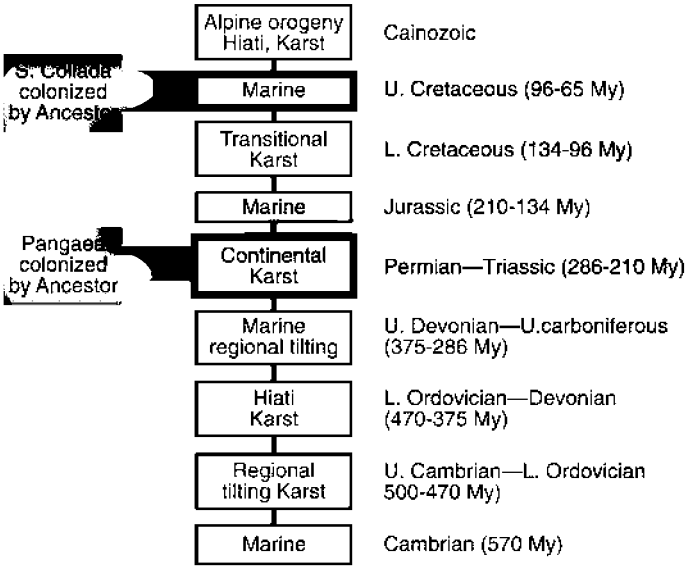



*Figure 4.* Simplified time flow diagram of the main geological events that took place in the study area.

trial influence, tentatively dated as Upper Cambrian-Remadocian (485–470 Myr) (Julivert and Martinez 1983). Later on, in a coastal environment, a thick sequence of sandstones was deposited during the Arenigian (485–470 Myr). A hiatus of more than 100 Myr separates the overlying Upper Devonian (375–360 Myr) unit from Areginian rock. Micro-conglomerates are found at the base due to the continental influence, and bioclastic limestones are exposed at the top. Even though the Lower Carboniferous sea covered the whole area (Tournaisian 360–350 Myr), black shales were deposited on an anoxic bottom. Marine conditions prevailed from the Viseian to the Lower Stephanian (360–300 Myr), as reflected by the dominant carbonate sedimentation. During the Stephanian (300–295 Myr), major terrigenous sedimentation occurred. During the Permian (295–245 Myr), terrestrial conditions dominated (with some marine incursions), as reflected by the presence of continental shales, sandstones, and conglomerates come rised of reworked Carboniferous limestones.

To the Triassic (245–205 Myr) record starts with continental red beds (Bunter) and gypsiferous shales (Keuper); intermediate marine limestone beds of Muschelkalk facies are lacking. Middle-Jurassic sediments (Liassic and Dogger) reflect a marine environment. The uppermost internal the Dogger and the Upper Jurassic (Malm), were periods of continental-dominated depositional environments.

The lower Cretaceous (145–97 Myr) sedimentation took place under continental or brackish conditions, but marine conditions prevailed once again

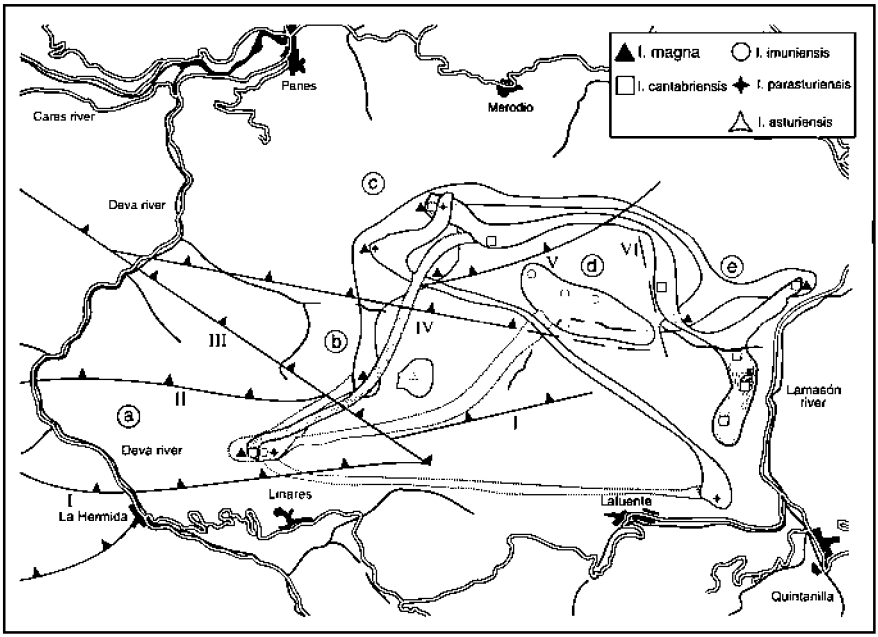



*Figure 5.* Boundaries in the Sierra de la Collada and areas bounded by faults. Distribution of *Iberobathynella* species.

during the Lower Cenomanian (97–90 Myr). Cainozoic sediments are not present in the study area.

From a palaeogeographical point of view, some tectonic markers were found:

- At the end of the Lower Cambrian regional tilting took place making karstification possible.
- The 100 Myr hiatus between the Arenigian and the Lower Devonian was a period of very important growth for the landmasses in the area, which later were submerged during the Carboniferous marine transgression.
- In the Late Hercynian (Permian-Lower Triassic), tensional processes gave rise to horst and graben structures, which provided favourable conditions for intense karstification. Marine conditions dominated during the Jurassic and Cretaceous, but isolated karstified landmasses remained.

Alpine Orogeny tectonics were responsible for the folding and thrusting of the rocks in the area. The plastic Upper Triassic (Keuper) beds were injected along fault surfaces to form impervious walls which temporarily isolated the karstic cells.

Additional information of the study area can be found in Gil Ibarguchi et al. (1983), Julivert and Martínez (1983), Capote and Carbó (1983), and Rincón et al. (1983). A general geological description of the Picos de Europa appears in Marquínez and Adrados (2002).

*Test of random distribution of bathynellid species in the Sierra de la Collada*

The original species/caves matrix (Table 1) includes the area to which each cave belong (letters 'a' to 'e') and whose faults are shown in Figure 2. This factorised matrix was analysed for faunistic similarity using the Bray-Curtis similarity measure. From the similarity matrix, a 2-D rank ordination was obtained using an MDS (Figure 6). Although it shows some homogeneous groups (e.g., 'd') this ordination has a certain degree of intermixing. The Anosim test was used to determine whether the caves in each area were closer to one another in terms of their fauna composition than to the caves of the neighbouring areas. If the faunal distribution was random among caves in an area, the within-area similarity would not be significantly different from the similarity among areas.

The value of $R$ was 0.606 ($p = 0.1\%$) for 999 permutations. Table 3 shows the results of the permutation test (randomly sampled with replacement) for pairwise comparisons, and their statistical significance. The global $R$ shows that the faunistic differences within caves belonging to the same area are smaller than those between caves in different areas, i.e., there is a non-arbitrary association between the fauna in caves in different areas. A detailed examinations of Table 3 shows caves in areas d and e, d and b, d and c to have significantly greater within-area similarity than between-area similarities. Areas d and a are the most different since they have the highest $R$ value (1). However, the $p$ value suggests it would be unwise to assume this is not due to chance. The other area pairs show low $R$ values that are not statistically significant.

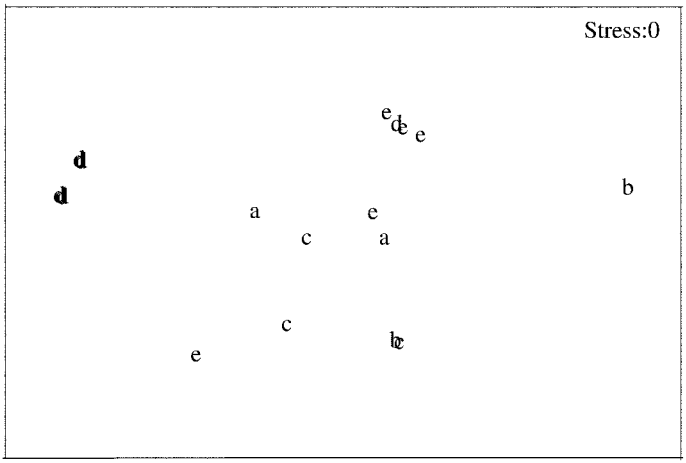



*Figure 6.* Two-dimensional ordination by MSD of caves based on faunal similarity. 'a' to 'e' are the sectors bound by faults in Figures 2 and 5. Each letter represents a cave in the sector.

*Table 3.* Pairwise comparison among sets of caves in different areas (sectors bound by faults)

| *R* | | Significance % |
|---|---|---|
| Groups | Statistic | |
| d, e | 0.806 | 0.1 |
| d, b | 0.909 | 4.8 |
| d, c | 0.875 | 0.8 |
| d, a | 1.000 | 16.7 |
| e, b | 0.584 | 8.3 |
| e, c | 0.184 | 10.3 |
| e, a | 0.320 | 25.0 |
| b, c | 0.143 | 26.7 |
| b, a | − 0.500 | 100.0 |
| c, a | − 0.208 | 60.0 |

*R* is a measure of difference within areas contrasted with differences between areas. An *R* value close to 1 indicates that the caves of an area are more similar to one another than to any cave of a different area.

### *DIVA analysis*

Figure 3 shows the DIVA results. If we assume that the distribution zone of the ancestors included the eight areas of our study, at least eight vicariant phenomena and 11 dispersions (as well as some extinctions) would be required to produce the nine species with today's distribution.

## Discussion

Within the general geo-palaeobiological framework of the Iberian Peninsula, conditions were favourable in the Lower Triassic, including a very large extent of marine domain (Figure 4), for the ancestor of the genus to colonize the continental environment. The common ancestor of the clade *Iberobathynella* must have been present on the margin of landmasses in coastal habitat of the Middle Trias (238 Myr) (Camacho et al. 2000) when the Iberian Peninsula, North America, and North Africa were still linked. This is the more plausible explanation for the existence on three continents of these phylogenetically close species that have no effective intrinsic dispersal mechanism. The Mesozoic continental split eventually broke up Pangea (Schram 1977), a vicariant event that may have been responsible for the divergence of the ancestral clade. Marine regressions (the second step of the 'Two-step Model' (Boutin and Coineau 1990; Coineau and Boutin 1992) and 'Regression Model Evolution', (Stock 1977, 1980) might help us understand how the ancestor arrived in the Sierra de la Collada, but they do not explain what happen after (Guil and Camacho 2001). Subsequently, the ancestor may have colonized this area of transitional karst-marine facies during the Upper Cretaceous (96–65 Myr) (see Figure 4). Successive cladogenesis (sister species) would have come about

through vicariance due to the emergence of new biogeographical barriers (faults) or local ecological events. This would be followed by greater of lesser dispersal on a small scale.

Tables 1 and 2 show that cave CO.209 has the greatest number of species – 4 of the 5 found in the area. Cave CO.275 has 3 species, 3 caves (CO.150, CO.220 and CO.277) have 2 species, and 14 caves contain only one.

The subgenus *I.* (*Asturibathynella*) is represented in the study area by 3 of the 9 known species in 10 of the caves distributed in the 5 areas bounded by fault lines (Figure5). The subgenus *I.* (*Espanobathynella*) was represented by 2 of its 3 species found in 12 caves in 4 areas (Figure 5). The species in this subgenus conserve more primitive traits than those of the other subgenus (see Figure 3).

*Iberobathynella* (*Espanobathynella*) is the least derived subgenus (5–7 nodes) in the proposed cladogram (Figure 3). The species *I.* (*E.*) *magna*, which has the most primitive characteristics (5 nodes) (Figure 3), was found in 7 caves in 4 areas of the study zone (Table 1, Figure 5) (area '*d*' was the only area where it was not found). This species is also found in its type locality (area '*g*') outside the study zone, and is the most widespread species of the 5 species groups. *Iberobathynella* (*E.*) *cantabriensis* shows the highest number of derived characteristics within the subgenus (7 nodes) (Figure 3). It was found in 9 caves in 3 areas, its distribution partially overlapping that of *I. magna* (not found in areas '*b*' and '*d*'). It appears to be endemic to the Sierra de la Collada. The intermediate species *I.* (*E.*) *espaniensis* (6 nodes) was only found in its type locality (area '*g*') outside the study area.

Having rejected a random allocation of the species in the caves and their different areas, it is tentatively proposed that fault lines caused the local fragmentation of the ancestor's original distribution, and that vicariant phenomena led to the differenciation of its populations. Geographical isolation eventually led to genetic isolation and clade divergence. The species with most primitive characteristics (*I. magna* and *I. cantabriensis*) might have been the first to colonize the more conservative interstitial (or karstic) freshwater environment (Boutin et al. 1992). They are found in more caves than any of the other species since they would have had more time to disperse.

The subgenus *Iberobathynella* (*Asturibathynella*) has the most derived species (8–11 nodes) (Figure 3). Within the subgenus *I.* (*Asturibathynella*), the species which conserves the most primitive traits is *I.* (*A.*) *imuniensis* (9 nodes) (Figure 3). This was found in 6 caves (Table 1) in the centre of the study area and in two additional areas (Table 2) (Figure 5). It also lives in other areas well away from the study zone (in Cantabria, Burgos and Huesca, see Figure 1) probably because it has been in the area long enough to reach many places that are easily accessible by passive dispersion (e.g., through watery environments). *Iberobathynella* (*A.*) *parasturiensis*, one of the species with the most evolved characteristics, is distributed on the eastern and southern periphery of the study zone, in 4 caves situated in 3 areas (Table 2), and was not found outside the study area. *Iberobathynella* (*A.*) *asturiensis* was only found in one cave (CO.044) (Table 2) (Figures 2 and 5) in the study zone (area '*b*') and outside

the zone of study in area '*g*'. Its rarity is probably due to its extinction in some intermediate areas (e.g., due to adverse ecological conditions) and perhaps because of it having had insufficient time or opportunity to colonize other accessible zones or to the occurrence of the speciation process in an habitat already isolated from other blocs; the resulting new species having never inhabited a wider area.

The faults and thrusting associated with the Alpine Orogeny during the Cainozoic could have been the vicariant process responsible for the cladogenesis which led to the appearance of the five sister species and their distributions.

Given the known phylogenetic and distribution patterns, the evolutionary palaeogeographic scenario suggested is only one of several possibles. There is a great deal of uncertainty at present regarding the phylogeny of *Iberobathynella*; the criterion used in this paper is only one of several possibilities. This phylogeny will gradually become more precise as new species are discovered and new populations found, etc. Secondly, further sampling will help refine the microdistribution of these five species in the Sierra de la Collada. Once the transgression/regression marine sequence (the second step of the 'two-step model of colonization and speciation' of Boutin and Coineau 1990; Coineau and Boutin 1992) of the shorelines (which alternate between those of the Tethys Sea and North Atlantic) led the ancestor of the five sister species to be established in the study area, local palaeogeographical events (Alpine Orogeny-linked) led to speciation followed by dispersions and small-scale extinctions. Unravelling the detailed history of these micro-picture processes might be a difficult business, but it is not very different from the task faced when trying to reconstruct those involved in any minimally complex macro-picture.

## Acknowledgments

We gratefully acknowledge the assistance of F. Molinero. We also thank Mark Creb and Adrian Burton for their help with the English translation. This study was supported by projects REN2000–2040 GLO, EVK2-CT-2001–00121 (PASCALIS, European Projects) and Convenio Junta Castilla y León- CSIC (2002–2004).

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